

ANATOMY OF THE TOMATO-WORM LARVA, *PROTOPARCE CAROLINA*.*

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The larvæ of *Protoparce carolina* are excellent subjects for the study of the anatomy of a developing insect. Its size and abundance during the late summer and early fall make it an available subject throughout the middle west. There are no detailed investigations of the larva of this family, so that a discussion, such as is given in the following pages, would not seem out of place. This investigation was started under Dr. A. D. MacGillivray, in order to acquire some information as to the internal anatomy of insects. Since there is such a dearth of literature dealing with the larvæ of American Lepidoptera, I have prepared, at his suggestion, the following descriptions and figures. I am greatly indebted to Dr. MacGillivray for suggestions and other help. I have found Mr. A. G. Hammer's excellent paper on the nervous system of the larva of *Corydalis cornuta* L. very useful and wish to express my appreciation of it.

METHODS.

When the work was first taken up, it was doubtful if it could be completed in one season, for only a limited amount of good material was available. There still remain a few points that need further observation, and these will be mentioned later. The best material for dissection proved to be larvæ that had been killed in hot water and preserved in 70% alcohol. Even with the largest and the best prepared specimens, one finds that the internal structures are not as easy to follow as one might expect. Especially is this true with respect to the nervous and circulatory systems. The factor causing the greatest difficulty outside of the frailty of the material, is the existence of a superabundance of adipose tissue or fat. To remove this fat, without tearing or destroying other parts, in order to observe the various organs, is difficult. The larvæ were opened by cutting a longitudinal slit along the meson on the dorsal or ventral aspects and laid out flat and pinned in dissecting trays. By gently rubbing and teasing the masses of adipose tissue, one can remove a sufficient amount to be able to observe the covered

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parts. Staining the tissues with a weak solution of Delafield's hematoxylin was found very useful in differentiating the finer structures. This was especially true in working with the nervous and circulatory systems. The resulting light-bluish coat given to the tissues, when not stained too deeply, proved to give the best results. Stained material will retain the stain for three or four days without becoming muddy and indistinct. To stain a certain area, the obstructing material was cleaned away and rinsed clean with running water. Pouring off all the water, two or three drops of the stain were dropped on the moist parts. The stain in no case was allowed to remain on the tissues over thirty seconds. As a general rule, the surplus stain was immediately washed off with running water.

The various parts of the larva will be discussed in the following order:—

A. External Anatomy:—Head, Thorax, and Abdomen.

B. Internal Anatomy:—Adipose Tissue, Digestive System, Silk Glands, Salivary Glands, Respiratory System, Muscular System, Circulatory System, Reproductive Organs, Wing Buds, and Nervous System.

A. External Anatomy.

The larva of *Protoparce carolina* when mature is approximately 9 cm. in length and 12–15 mm. in diameter. It has a distinct greenish cast with diagonal lines of dark brown, pigmental blotches, which extend from the dorso-caudal part of each abdominal segment ventro-cephalad. The body is divided into three regions, head, thorax, and abdomen.

HEAD (Figs. 1, 2 and 3).—The head is the smallest division of the body. It is a non-wrinkled, yellowish-white region, which from a lateral or ventral aspect is oval in outline, while from a cephalic view, it is spherical. On the median portion of the cephalic aspect, there exists a distinct inverted Y-shaped suture (*e*), the epicranial suture, which divides the fixed parts of the head into three regions. Connected with the ventral part of the region included within the arms of the Y, are the mouth parts. The large areas laterad of the epicranial suture have on their ventral aspects the antennæ and simple-eyes.

Eyes.—The simple eyes (*o*) consist of two groups of six ocelli, five of which are arranged in a semicircle with the sixth on the median part of the diameter of the circle. These groups

viewed from the cephalic aspect, are on the ventro-lateral regions of the head.

Antennæ.—Mesad and slightly ventrad of the ocelli are located the three-segmented antennæ (*at*). Each consists of a conical-shaped basal segment bearing on its distal end two similar, cylindrical segments. On the distal end of the third segment, two unequal setæ are borne, the mesal one being the longer.

Front.—The triangular area included within the arms of the Y, is the front (*f*).

Clypeus.—The clypeus (*cl*) is attached to the ventral edge of the front and forms a transverse bar, bearing a single seta on each lateral end.

Labrum.—At the apex of the clypeus, there is borne a bilobed area (*lr*), which has on its ventral edge a deep notch, which makes the labrum bilobed. On the lateral and ventral parts of these lobes are borne setæ. Three large setæ for each lobe seems to be the constant number in the various specimens examined, while there is a variation in the number of small setæ on the depressed region above the notch.

Mandibles.—The two stout mandibles (*md*) meet in a zigzag line caudad of the labrum. The zigzag line is due to the interlocking of the four dark, tooth-like projections which occur on the mesal edge of the laterally opening mandibles. The mandibles are connected to the head proper at the lateral margins of the labrum and maxillæ. Each mandible bears on its distal median portion a single seta.

Maxillæ.—Directly caudad of the proximal portion of the mandibles are two globular maxillæ (*mx*), each of which bears ventrally a three-segmented, tapering palpus. The distal segment of the palpus is very small.

Labium.—Mesad of the two maxillæ, there is a wedge-shaped labium (*lb*), which gives rise to a tubular projection at its caudo-distal edge.

Spinneret.—This tubular projection (*i*), which extends caudad and ventrad, is the spinneret, from which the silk is exuded.

THORAX.—The thorax, being the second region of the body, is adjacent to the head and consists of three segments as follows:

Prothorax (Fig. 1).—The prothorax is the cephalic segment of the thorax and is comparatively smooth and not transversely

wrinkled on its dorsal aspect. It bears on its ventral side a pair of true legs. On the caudal part of the lateral surface of the prothorax can be seen an oval spiracle.

Mesothorax and Metathorax (Fig. 1).—The mesothorax and metathorax are very similar, consequently the description of either will answer for both. Six, transverse furrows cut the dorsal surface of each segment and a pair of true legs is found on the ventral aspect of each. These two segments bear no spiracles.

Legs (Figs. 1lg and 5).—The three pairs of legs on the thorax are approximately alike. On all these legs numerous small setæ are borne. A leg consists of the following parts. At the base of each leg is a widened, oval, furrowed area, which constitutes the coxa (*co*) of the leg. The trochanter (*tr*), a wedge-shaped, darkened sclerite, exists on the ventro-mesal margin of the coxa adjacent to the following segment of the leg, the femur. The femur (*fe*) is the large, cylindrical segment distad of the trochanter. The tibia (*ti*) follows the femur and bends slightly mesad. The distal segment of the leg is a small, cone-shaped tarsus (*ta*), which bears on its distal end, minus an intervening suture, a single, dark-hooked claw (*ca*).

ABDOMEN (Fig. 1).—The abdomen is by far the largest portion of the larva, for it consists of eight, possibly nine, large segments. Some writers consider the eighth segment, as it is here called, as made up of two segments. The proleg (*a. pl*) of the last segment in this case would be attached to the ninth, while the anal horn (*ah*) would be borne on the caudo-dorsal part of the eighth segment. In the abdominal segments one to seven, a distinct similarity exists. However the abdominal segments three, four, five and six, give rise to pairs of prolegs (*pl*).

Fourth Abdominal Segment (Fig. 1).—Taking the fourth abdominal segment as a typical segment, one finds it is composed of eight, distinct, transverse, ridges on its dorsal and dorso-lateral aspects. Numerous pigmental areas can be found in the furrows. The most striking pigmental arrangement is the diagonal line of spots running from the dorso-caudal angle of the segment toward the ventro-cephalic portion. The large, oval spiracles (*s*) are located on the lateral aspects of the segments in the ventral and cephalic portion. These oval, darkened areas (Fig. 6, *s*) on magnification appear to be made up of a fine network of dark chitin and also show an indefinite,

median, dorso-ventral slit, which opens into the trachea. The prolegs (*pl*) on the ventral aspect of this segment, are a pair of fleshy appendages, which bear on their distal margins a convex, double row of black hooks, which point mesad (Fig. 4).

Eighth Abdominal Segment (Fig. 1).—The last segment of the abdomen is somewhat elongated and not so excessively cut by transverse furrows as the preceding segments of the abdomen. At the middle of the dorsal surface of the segment, a spine-like anal horn (*ah*) arises. From this point the segment is cut off obliquely at an angle of 45°. At the dorsal edge of this sloping portion the triangular anal plate (*ap*) is located. The anus (*a*) is situated ventrad of the anal plate. The anal prolegs (*a. pl*) resemble in most details the prolegs of the fourth abdominal segment. However their size is a trifle larger and the relation of their connection with the ventral surface of the segment is somewhat different. The spiracle (*s*) of this segment may be seen in its usual position.

B. Internal Anatomy.

ADIPOSE TISSUE.

On opening a larva, the first thing noted is the abundance of fat, or adipose tissue (Fig. 10). Adipose tissue, as seen throughout the body, is the white, flocculent, lobulated, ribbon-like material surrounding and adjacent to the various organs in the body cavity. This fat tissue is stored up for future metamorphosis. Sections and mounts of adipose tissue stained with eosin show (Fig. 10) its oily nature. The large spherical, fat cells in their crowded, massed condition assume a polygonal form. Internally, the cells are filled with oily globules of fat and possess also a dark-staining, centrally located nucleus. To rid the larva of this fat, one needs carefully to rub and tease it loose.

ALIMENTARY CANAL.

Extending from the mouth to the anal opening of the larva, there is a long, straight, locally constricted tube, which in the abdominal region occupies the greater portion of the body cavity. This is the alimentary canal, or digestive tract. On opening a larva from the dorsal aspect (Fig. 7), the following structures may be observed:—

Pharynx (Figs. 7, 8, and 18).—The pharynx (*p*) is the smallest part of the digestive tract and is located at the extreme

cephalic end within the head. It proceeds from the ventrally-located, mouth opening, dorsad and caudad till it enlarges into a region called the œsophagus. The more or less distinct flexure in the pharynx occurs for the most part caudad of the two head ganglia. The abruptness of this flexure depends in great part upon the position of the head. The pharynx as represented in the figures has been straightened. Arising from the pharynx are bundles of muscles that attach themselves to the head capsule.

Œsophagus.—As the pharynx begins to widen caudad of the flexure within the head, the œsophagus (*œ*) here begins and extends caudad to the ventriculus (*ve*), which is in the cephalic region of the metathorax. This trumpet-shaped piece has a finely, transversely striated ectal surface.

Ventriculus.—The ventriculus (*ve*), is a long, straight, large, transversely folded tube, which extends from the caudal end of the œsophagus to the caudal portion of the sixth abdominal segment. The transverse, folded, outer covering of the ventriculus is divided into six areas by means of six fine, longitudinal bands of muscles, which extend the full length of the ventriculus. The six bands have the following positions. One band is dorsal along the meson, one ventral along the meson, two dorso-lateral, and two ventro-lateral.

Gastric Cæca.—Located at the dorso-cephalic end of the ventriculus, between the terminations of the muscle bands, there are four groups of small, white, rounded bodies (*ce*), the gastric cæca.

Small Intestine.—Caudad of the smooth, slightly converging, caudal end of the ventriculus, there is a distinct constriction, which is immediately followed by a small ring-shaped area, the small intestine (*s. i.*) On the ectal surface of the small intestine, pits exist through which tracheæ and muscles fibres-enter. From the ventral aspect, two small bladders may be seen, which enter the small intestine at its latero-cephalic portions.

Large Intestine.—The smallest constriction in the caudal region of the alimentary tract, which is just caudad of the small intestine, is the beginning of the large intestine (*l. i.*). Immediately following this middle constriction there is a flaring shoulder, which again becomes constricted caudad, but not to as great an extent as the constriction just described. Two more small, shoulder-like areas follow this constriction, the

anterior one being very slight. This constitutes the large intestine. The above shape and form holds true only when the intestine is completely empty and relaxed. Excreta within will cause the large intestine and rectum, which follows, to assume various shapes.

Suspensory Muscle of the Large Intestine.—These two muscles (*s. m.*) extend from the ventral side of the cephalic margin of the caudal enlargement of the large intestine to the latero-ventral portion of the transverse conjunctiva, between the sixth and seventh abdominal segments. These two cord-like muscles can be best seen from the ventral aspect.

Rectum.—The rectum (*re*) is the caudal termination of the alimentary canal and occupies the caudal portion of the seventh abdominal segment and the entire portion of the eighth. The rectum is the largest in diameter of all the portions of the alimentary canal. On the dorsal surface of the rectum, there are located two prominent, longitudinal bands of muscles that converge at the cephalic end of the rectum and connect at their caudal end to the body wall. By means of the contraction of the rectum, the characteristic form is given to the excreta of lepidopterous larva.

Tracheæ of the Alimentary Canal. (Fig. 7, *t*).—The tracheæ of the oesophagus and pharynx are very small and their arrangement is difficult to trace. From the adjacent first six abdominal spiracles there is a fan-like arrangement of tracheal branches which enter the lateral, folded area of the ventriculus. These tracheæ support the ventriculus and supply it profusely with air. Tracheæ from the seventh abdominal segment lead to the large and small intestine and the cephalic area of the rectum. However, the rectum obtains most of its oxygen by means of the tracheæ coming from the eighth abdominal segment.

URINARY SYSTEM.

The urinary system (Figs. 7 and 9) of *Protoparce carolina* is composed of two bladders, right and left, and their respective tubules. Fig. 9 shows a bladder (*b*) and how it enters the anterior part of the small intestine on the ventro-lateral portion. It has been pulled out of its normal position in order to show the place of attachment of the bladder with the small intestine. It turns back on itself, as in Fig. 7, and thus conceals its place of entrance. Leading cephalad from the small, delicate, white

bladder, there is a common duct, which splits immediately and gives rise to two branches; one continues cephalad on the ventral side (*v. m. t.*), while the other passes dorsad and divides into two branches (*d. m. t.*), both of which proceed cephalad along the dorso-lateral part of the ventriculus. Tracing a ventral Malphigian tubule, we find that it extends cephalad in a nearly straight line, adjacent to the ventro-lateral portion of the ventriculus to the second abdominal segment. At this point it turns abruptly back and continues caudad and parallel with itself until it reaches approximately the seventh abdominal segment, where it becomes very convoluted and soon loses itself in the mass of convoluted, terminal, Malphigian tubules and adipose tissue. The pairs of dorsal tubules proceed cephalad and parallel into the second and third abdominal segments. The mesal tubule of the pair within the third abdominal segment, turns mesad and caudad, while the lateral tubule turns laterad and caudad within the second abdominal segment. After turning, both tubules proceed caudad and parallel with their cephalad-extending portion until they reach the sixth abdominal segment, where they turn laterad and continue into the seventh abdominal segment soon to become highly convoluted and intertwined with the ventral, terminal tubules and adipose tissue. The tubules are easily detected not only from their position, but from their form. They appear like long, white, knotted strings. The proximal portion of a tubule is more or less flattened and consists of scattered, white, globular nodules. As a tubule proceeds distad, the nodules become more frequent until finally at the terminal part of a tubule, as it enters the seventh abdominal segment, the tubule consists of a series of closely packed, irregularly arranged nodules. It was impossible to determine the termination of a tubule on account of the intertwining of the tubules, their delicate consistence, and the ever present adipose tissue.

SILK GLANDS.

Running along each side of the lateral portions of the ventriculus (Fig. 7, *sg*) and imbedded in the adipose tissue of the lateral body wall, are two opaque, smooth, yellowish-white cords. These two cords are the silk glands. They extend from the base of the spinneret on the labium into the seventh abdominal segment. The right and left silk glands of this larva

are practically of the same size throughout their length. However, the cephalic end from the metathoracic region to the point of attachment to the spinneret is much smaller and serves probably only as a conducting tube. These conducting tubes can be traced into the head until they reach the chitinous projections on the caudal margin of the head, around which they bend at right angles and unite on the meson. Farther than this the duct was not traced. As one traces, caudad from the metathoracic region, a silk gland proper, one sees the beginning of the coiled or rather convoluted portion of this organ. Within the fifth and sixth abdominal segments the convolutions are most abundant. The gland terminates in the mass of Malpighian tubules and adipose tissue within the seventh abdominal segment.

SALIVARY GLANDS.

The two salivary glands (Fig. 7, *sl*) appear as delicate, white, nodulated, twisted tubes on each side of the pharynx and œsophagus. They extend from the anterior portion of the head to the region of the metathorax and here end within a flattened mass of adipose tissue on the ventral wall of the thorax marking the line of division between the mesothorax and the metathorax. Tracing a gland into the head, it follows along the space between the muscles and the lateral margin of the pharynx to the margin of the tendon of the adductor muscle of the mandible, where it becomes much reduced in size.

RESPIRATORY SYSTEM.

In the discussion of external anatomy, it was noted that there were nine spiracles, eight of which were abdominal and one thoracic. Opening a larva from the ventral side and removing the alimentary canal and a part of the adipose tissue, a system of more or less transparent, white, smooth tubes, similar to Fig. 11, reveals itself. To follow the tracheæ with most satisfactory results, one should open a freshly killed larva and immerse the same in water. In this case the tubes would be filled with air and appear as glistening, silver cords.

Arising from each spiracle, there is an immense, bush-like mass of tracheæ, that branch into many fine tubes, which in most cases extend to the various parts, such as muscles, nerves, alimentary canal, legs, heart, etc., of the same body segment. This holds true of the abdominal segments only. All the

spiracles of each side open into the main, longitudinal trachea which extends between the spiracles and is amply long to allow for expansion of the body segments. A unique fact, to note in regard to these connecting tracheæ, is that each gives rise to small lateral branches varying from two to six or more in number.

In examining specimens for transverse tracheal connections between spiracles of the same segment, none were found on the dorsal aspect except from the thoracic spiracle and the eighth abdominal spiracle. If other dorsal cross tracheæ exist, they must be very minute and delicate, for they were carefully sought. In the case of the eighth abdominal segment, only one minute dorsal cross trachea was found (Fig. 11), while in the prothoracic region, two distinct, cross tracheæ were observed, the cephalic one being the larger and giving rise to two pairs of tracheæ, which proceed cephalad and ventrad into the anterior portion of the head. The caudal cross trachea of the two gives rise to four or five minute pairs of tracheæ, which diverge in various directions. It should be mentioned, that the tracheal system varied considerably in minor details in different specimens. Looking on the ventral aspect for cross tracheæ, it was found that a small cross trachea existed near each ganglion of the nervous system (Fig. 13) except the supra-oesophageal ganglion, which is located dorsad and cephalad of the pharynx. The cross tracheæ adjacent to the metathoracic and mesothoracic ganglia seemed to originate from branches of the connecting tracheæ between the first and second spiracles of the body. In all cases, with one exception, the cross tracheæ lie ventrad of the nerve cord and in the abdominal region caudad of the ganglia. The one exception is the cross trachea that lies adjacent to the suboesophageal ganglion. In this case the trachea is dorsad of the commissure (*H. 2g.*). Each cross trachea on the ventral aspect gives rise to a pair of tracheæ that supplies the adjacent ganglion.

MUSCULAR SYSTEM.

In the gross treatment of the muscular system (Fig. 12) of this larva only the more prominent bands of muscles will be mentioned. The muscular system of the larva is segmentally arranged. The muscle fibres are confined in their extent to a single segment and furthermore the muscular arrangement is similar in each segment on the whole. This is especially true

with the abdominal segments. Consequently the description of a single segment will answer as a type of all the segments. The muscles of the thorax are more complex, due to the muscles of the legs.

Great Dorso-Recti Muscles (g. d-r.m.).—The broad area of white, opaque muscles lying to the right and left of the heart are the great dorso-recti muscles. Upon a superficial examination of the ends of the muscles at the conjunctiva, one might be led to think that the muscles were continuous, except for a slight depression. But as a matter of fact, they are contiguous and separated by a narrow, hyaline, cuticular line at the point of the depression. These particular muscles attach themselves to the cephalic side of the transverse conjunctiva.

Small Dorso-Recti Muscles (s. d-r. m.).—Laterad of the lateral margin of the great dorso-recti muscles, the small dorso-recti muscles are located. This band of muscles consists of three to five small fibres that are fastened to the caudal margin of the transverse conjunctiva. Laterad of this bundle of muscles an area exists, which is free of longitudinal muscles but contains the spiracles and their accompanying tracheæ.

Great Ventro-Recti Muscles (g. v-r. m.). If the larva is spread out as in Fig. 12, the large band of muscles laterad of the free area consists of the great ventro-recti muscles. This group is ventrad of the spiracles. These muscles attach themselves to the cephalic aspect of the transverse conjunctiva.

Small Ventro-Recti Muscles (s. v-r. m.).—These muscles are located mesad of the great ventro-recti muscles along the ventral area of the larva adjacent to the nervous system. They are attached to the caudal side of the transverse conjunctiva. All these muscles are supplied by tracheæ.

Dorso-Ventral Muscles (d. v. m.).—The dorso-ventral muscles are the two groups of short muscles that extend dorso-ventrad across the free area existing between the great ventro-recti muscles and the small dorso-recti muscles, one group at the cephalic end of the segment and the other at the caudal end. Two fibres, the cephalic group, cross immediately cephalad of the spiracle and mesad of the longitudinal trachea between the abdominal spiracles and mesad of the small dorso-recti muscles. The other remaining fibres disappear dorsally in the cephalic part of the segment as the two already described fibres but ventrally they cross at an angle the transverse conjunctiva

and disappear from view in the extreme caudal part of the preceding abdominal segment. Other muscles besides those thus far discussed are present in each body segment. By carefully lifting the longitudinal fibres, one finds other bands of muscles running at an angle to those named above. This is indicated in Fig. 12, (*x*), where in the caudo-dorsal angle of the free part about the spiracles in each segment one sees the ends of such diagonal bands.

CIRCULATORY SYSTEM.

Dorsad of the alimentary canal is a long slender tube (Fig. 12) embedded to some depth in a mesal cavity of adipose tissue between the right and left bands of the great dorso-recti muscles. This tube, which comprises the whole of the enclosed circulatory system, extends from the eighth abdominal segment to and within the head. The enlarged part of this tube, extending from the eighth abdominal segment into the meta-thoracic region, is the pulsating organ, the heart.

Heart.—The heart (*h*) is a very delicate, flattened, muscular tube closed at the caudal end and presumably opening in each segment by a system of valves. Owing to the lack of fresh and living material the valves of the heart were not studied. After injecting some colored fluid into fresh specimens, the valves should readily show themselves.

Wings of the Heart.—Within the area of the first to the fifth abdominal segments, four pairs of laterally extending fan-like rays of tendons (*w. h.*) are seen. The tendons extend from the ventro-lateral edges of the heart and converge at the point where the three anterior dorso-ventral muscles penetrate between the great dorso-recti muscles and the small dorso-recti muscles. The wings are composed of connective tissue and muscle fibres, connecting themselves to the body wall beneath the small dorso-recti muscles. The function of the wings of the heart is probably to protect the heart from the peristaltic movements of the alimentary canal. Between successive fans the heart proper is distinctly constricted. In these regions without much doubt the valves of the heart are located. The caudal part of the heart, extending from the midportion of the fifth abdominal segment to the caudal end, is supported by scattered, irregularly arranged tendons on the ventral surface, that attach themselves to the nearby body wall.

Aorta.—The cephalic extension of the heart, the aorta (*ao*), starting within the metathoracic region and passing into the head, is a much smaller and smoother muscular tube. It runs close to the dorsal surface of the œsophagus and the pharynx and finally terminates with a slight dilation after it has passed beneath the supra-œsophageal ganglion (Fig. 8 and 18). This location of the outlet allows a constant and abundant supply of fresh blood within the head region. The mouth-like opening of the aorta is held in its characteristic position by means of tendons that connect themselves to the head capsule (Fig. 8).

The heart, like the other organs of the body, is well supplied with air tubes. The arrangement of the heart-tracheæ is shown in the fifth abdominal segment (Fig. 12).

REPRODUCTIVE ORGANS.

After examining numerous specimens for gonads, two white, opaque, ovate bodies (Fig. 12, *r*) were found on each side adjacent to the heart in the fifth abdominal segment. Difficulty was experienced in locating these organs on account of their close similarity to adipose tissue and their being embedded in the same. It was impossible to determine the sex of the glands on account of the limited material at hand. From the fifth abdominal spiracle, tracheæ arise that supply the reproductive organs.

WING BUDS.

The wing buds (*f. b.* and *h. b.*) are the histoblasts, imaginal discs, or imaginal buds of the future wings of the adult insect. They are formed as invaginations of the hypodermis, to which they are attached. They are small, kidney-shaped bodies located in the dorso-lateral portions of the mesothorax and metathorax. If a larva is cut along the ventral meson, the wing buds will be seen about midway between the meson and the outer cut body wall. Two tracheæ enter the wing buds at their base, one into the caudal portion and the other into the cephalic portion.

NERVOUS SYSTEM.

The nervous system (Fig. 13) of *Protoparce carolina* consists of a long, white cord, knotted at segmental intervals, which extends for the most part along the meso-ventral portion of the body. This ventrally located, simple nervous system is made up of three parts: ganglia, commissures, and nerves. The

enlarged, oval knots, found in each segment of the body, are the ganglia. Only one ganglion exists in each body segment outside of the head and the seventh and eighth abdominal segments. The cords running between the ganglia, which in some cases are double or partially so, are the commissures. The nerves are the branches of various sizes extending from each ganglion and in some cases from the commissures. These fine threads permeate all parts of the body. The nervous system will be discussed under the following divisions: Abdominal Ganglia, Thoracic Ganglia, Head Ganglia, and Sympathetic Systems of the Head.

ABDOMINAL GANGLIA (Fig. 14 and 15).—The abdominal ganglia are the simplest in type. The distinct similarity between the first six abdominal ganglia makes it possible for one description to answer for all. The seventh and eighth abdominal ganglia will be discussed under a separate heading.

First Six Abdominal Ganglia (Fig. 15, A. 1g).—The first six abdominal ganglia are located in the middle or cephalic part of each abdominal segment and consist of the following parts:—

Lateral Nerves.—The lateral nerves (*l*) are the two branches, which arise from the cephalic part of the lateral margins of the ganglia and innervate the latero-dorsal portion of the body.

Ventral Nerves.—Directly caudad and slightly ventrad of the lateral nerves, the ventral nerves (*v*) arise and extend caudo-laterad to innervate the ventral area of the body segments. Near the point of entrance of the ventral nerves, a pair of small nerve-like tracheæ enter the ganglia. These two tracheæ, one on each side, are derived from the transverse tracheæ located in each abdominal segment ventrad of the nerve cord. The tracheæ can be distinguished from the nerves by staining with Delafield's hematoxylin as heretofore advocated. A stained trachea is more deeply colored than a nerve and also shows its distinct ringed nature on high magnification.

Ventral Sympathetic System (Fig. 15, *m.* and *t. n.*).—Extending between the ganglia there is a single, large, white cord, the commissure. Just before the commissure enters the cephalic end of a ganglion, it divides into two cords or is furrowed on the dorsal surface. The ventral sympathetic nerves arise from the cephalic end of this fork. With some of the ganglia, this forking or splitting of the commissure is not very great but can in each case be detected.

Median and Transverse Nerves.—The median nerve (*m*) arises from the commissure at the cephalic end of this inverted V-shaped split and extends caudad for a short distance. At its caudal end near the ganglion, it forks and gives rise to two transverse nerves (*t. n.*), that extend in opposite lateral directions and more or less parallel with the lateral nerves. In the short distance in which the transverse and lateral nerves are parallel, the transverse nerves give rise to a web of nerve fibres (*px*), which connect with the lateral nerves and the ganglion. Beyond this web or plexus, the transverse nerves diverge from the lateral nerves in a cephalo-lateral direction.

Ganglia Seventh Abdominal Segment. (Fig. 14, *A. 7* and *8 g*).—Within the seventh abdominal segment, is a double ganglion, or rather two ganglia, but no visible commissure connects the two because of the close approximation of the ganglia. This modification brings about a change in the nerves.

Seventh Abdominal Ganglion.—The seventh abdominal ganglion is comparable to the ganglia of the first six abdominal segments. It gives rise to nerves arranged in the same manner and does not need further description.

Eighth Abdominal Ganglion.—The elimination of the commissure between the seventh and eighth ganglia has not only brought the ganglia together but has lengthened as well as changed the place of origin of the nerves from the ganglion.

Lateral Nerves.—The comparatively large lateral nerves (*l*) arise not from the lateral margin of the ganglion but from its dorso-caudal end and extend with a slight divergence far into the eighth abdominal segment before branching.

Ventral Nerves.—Ventrad and slightly laterad of the lateral nerves, there arises a small pair of ventral nerves (*v*), which also extend into the eighth abdominal segment before branching. Adjacent to these ventral nerves the accompanying tracheæ, which resemble nerves closely enter the ganglion. The ventral trachea of the eighth abdominal segment, however, still exists in its normal position within the eighth segment. This elongates to a great extent the pair of tracheæ that arise from it to supply the eighth abdominal ganglion.

Ventral Sympathetic System (Fig. 14, *m.* and *t. n.*).—The fusing of the seventh and eighth abdominal ganglia causes the sympathetic system apparently to arise from the dorso-caudal end of the seventh abdominal ganglion.

Median and Transverse Nerves.—The median nerve (*m*) arises from the mid-dorsal area of the double ganglion. It is very short. On teasing apart the two ganglia, the median nerve remains attached to the caudal end of the seventh abdominal segment. It immediately gives rise to its pair of transverse nerves (*t. n.*), which extend caudo-laterad into the eighth abdominal segment more or less parallel to and laterad of the pair of lateral nerves. However, no plexus exists between the transverse and lateral nerves of this ganglion, as was noted in the other segments.

THORACIC GANGLIA (Fig. 17, *T. 1g*, and *T. 2g*, Fig. 16, *T. 3g*).—The thoracic ganglia are three in number, the mesothoracic and metathoracic ganglia are similar in form.

Mesothoracic and Metathoracic Ganglia (*T. 2g* and *T. 3g*).—The mesothoracic and metathoracic ganglia are slightly larger than the abdominal ganglia and are not as far apart. Extending from the caudal ends of all the thoracic ganglia, there is a large commissure (Fig. 17) which, in case of the prothoracic and mesothoracic, proceeds but a short distance and then forks and forms the diamond-shaped area in which the ventral sympathetic nerves are located. In both cases, the diamond-shaped area between the metathoracic and mesothoracic and between the mesothoracic and prothoracic ganglia occupies about two-thirds of the distance between the ganglia.

Lateral Nerves.—The lateral nerves (*l*) proceed from the ganglia at their latero-cephalic part and are adjacent to the lateral edges of the commissures. The lateral nerves extend in a latero-cephalic direction.

Connective Nerves.—The connective nerves (*c. n.*) arise from the lateral edges of the commissure and extend in a caudal direction. In the case of the diamond-shaped area between the mesothoracic and metathoracic ganglia, the connective nerves arise midway between the anterior and posterior angles of the diamond. While, with the diamond-shaped area between the prothoracic and mesothoracic ganglia, the commissure gives rise to its connective nerves very much nearer the mesothoracic ganglion than to the anterior end of the opening. The connective nerves proceed a short distance caudad, then turn laterad and somewhat cephalad, and soon fuse with the lateral nerves laterad of their connection with the commissure. Before fusing with the lateral nerves, the connective nerves give rise

to a branch that extends cephalad and somewhat parallel with the lateral nerves. This branch soon forks, one branch extends laterad across the lateral nerve, the other branch cephalo-laterad and parallel with the lateral nerve.

Ventral Nerves.—In the mesothoracic and metathoracic ganglia, the ventral nerves (*v*) arise from the lateral margin of each ganglion in a plane ventrad of the lateral nerves. The metathoracic, ventral nerves extend cephalo-laterad, while the ventral nerves of the mesothoracic ganglion project directly laterad. In both cases the ventral nerves innervate the ventral portion of the body. At the point of entrance of the ventral nerves, one finds the usual tracheæ that supply the ganglion with air.

Ventral Sympathetic System (Fig. 16, *T. 3g*, Fig. 17, *T. 2g*).—With the mesothoracic and metathoracic ganglia, the ventral sympathetic consists of a median nerve and transverse nerves.

Median and Transverse Nerves.—The median nerves (*m*) arise from the commissure in the cephalic angle of the diamond-shaped areas and in both cases are of considerable length before the fork. The mesothoracic median nerve is longer than the metathoracic median nerve. In both cases the transverse nerves (*t. n.*), after arising from the caudal end of the median nerve, proceed in such a direction as to cross the commissure at the point near where the connective nerves arise. After crossing the commissure, they tend to take, as usual a course parallel to the lateral nerves. The web or plexus (*px*) of nerves in these two ganglia is very distinct; this is especially true in the metathoracic ganglion. The plexus occurs principally in the triangular area between the commissures, the lateral nerves, the transverse, and the connective nerves. In Fig. 17 (*T. 1g*, *T. 2g*), one may note a dark line drawn from the median portion of the prothoracic ganglion caudad. The true connection and relation of this nerve-like thread was not determined.

PROTHORACIC GANGLION (Fig. 17, *T. 1g*).—The prothoracic ganglion is very similar in form and in the arrangement of its nerves to the abdominal ganglia. As heretofore mentioned, the commissure, which projects caudad from the prothoracic ganglion, is simple and large. The ganglion cephalad of the prothoracic ganglion is the subœsophageal ganglion and is located only a very short distance from the prothoracic ganglion.

The commissure extending between these two ganglia fail to unite before entering the caudal end of the subœsophageal ganglia; consequently the two ganglia are connected by two distinct parallel strands.

Lateral Nerves.—The lateral nerves (*l*) are the two branches which arise from the cephalic part of the lateral margins of the ganglion. These nerves soon divide into many small branches and innervate the lateral areas of the prothorax.

Ventral Nerves.—The ventral nerves (*v*) project from the caudo-lateral margin and are accompanied by the usual pair of tracheæ. In this ganglion however, the ventral nerve of each side is not single but is composed of two small branches.

Ventral Sympathetic System.—With the prothoracic ganglion, the customary median and transverse nerves are wanting but the following new arrangement exists:—

Subconnective Nerve (Fig. 17, *T. 1g*).—Dorsad and cephalad of the prothoracic ganglion, the large subconnective nerves (*sn*) exist, which cross the commissure. Within the region adjacent to the ganglion, a plexus or web of nerves (*px*) extends between the subconnective nerve, the ganglion, and the proximal ends of the lateral nerves.

GANGLIA OF THE HEAD (Fig. 17, *H. 1g* and *H. 2g*, Fig. 18).—In the alimentary tract as it extends to the mouth by means of the pharynx, there is to be noted a distinct flexure in the head. The two head-ganglia are located slightly distad of this flexure. The corresponding flexure in the nervous system is located between the subœsophageal and prothoracic ganglia. The two head-ganglia rest on the pharynx but on opposite sides (Fig. 18). The more distal ganglion, the supraœsophageal (*sp*), is cephalad of the pharynx and entad of the front of the head capsule. The subœsophageal ganglion (*su*) is caudad of the pharynx and connected to the supraœsophageal by means of two commissures, which together with the two ganglia form a complete ring about the pharynx.

Suboesophageal Ganglion (Fig. 17 and 18, *su*).—The subœsophageal ganglion is located caudad of the pharynx and in a plane ventrad of the supraœsophageal. It gives rise to the following nerves:—

Crura Cerebri.—The crura cerebri (*c. c.*) arise from the cephalo-ventral portion of the lateral margin of the subœsophageal ganglion very close to the pharynx. This pair of large

cords arising from the lateral margins help to complete the circle about the pharynx by connecting themselves to the latero-caudal portions of the supraœsophageal ganglion.

Mandibular Nerves.—Adjacent to the crura cerebri and extending in a caudo-mesal direction, there arises a pair of nerves (*md. lb. n.*), which are of approximately the same size as the crura cerebri. These nerves extend ventrad and divide into two nerves of unequal size; the larger nerve (*md. n.*) proceeds cephalad and ventrad and innervates the mandible.

Labial Nerves.—The labial nerves (*lb. n.*) arise from the mesal side of the mandibular-labial nerve (*md. lb. n.*). They extend ventro-caudad and innervate the labium.

Maxillary Nerves.—Caudad and adjacent to the mandibular nerves, the maxillary nerves (*mx. n.*) arise. They are smaller and soon branch and innervate the maxillæ.

Unidentified Nerves.—Caudad and slightly dorsad of the maxillary nerves, there arises on each side a nerve of considerable size (*z*), which extends laterad into the muscles of the head toward the salivary ducts but I have been unable to determine what they innervate.

Ventral Nerves.—From the mid-lateral area of the ganglion, the ventral nerves (*v*) project accompanied by their accustomed tracheæ. In this ganglion a light stain brings out very successfully the branches of the tracheæ (*t*) as they radiate over the surface of the ganglion. The ventral nerves in this case project dorso-caudad into the caudal part of the head.

Supraœsophageal Ganglion (Fig. 17 and 18, *sp*).—The supraœsophageal ganglion (*sp*) is the largest ganglion of the nervous system and is located on the cephalic surface of the pharynx. The transverse diameter of the ganglion is about twice that of the ventro-dorsal diameter. The ganglion is constricted along the meson into two lobes. The following nerves arise from this ganglion:—

Crura Cerebri.—The two large crura cerebri (*c. c.*) that proceed from the subœsophageal ganglion in a dorso-cephalic direction, connect with the supraœsophageal ganglion on the latero-dorsal margins. The two trunks are comparable to the commissures that extend between the ganglia in other regions of the body. Just dorsad of where the crura cerebri arise from the supraœsophageal ganglion, a large trachea enters the ganglion on each side of the head. These tracheæ, a short distance from

the ganglion, fork, one branch extending ventrad and the other more or less dorsad. These particular tracheæ arise from branches that lead into the head from the spiracle located in the prothorax.

Subœsophageal Commissures.—The subœsophageal commissures (*s. c.*) are the branches that arise from the ventral side of the crura cerebri near the supraœsophageal ganglion. These two branches encircle the pharynx. On the caudal part of this semicircle two small branches occur which extend dorsad and innervate the large muscle fibres of the pharynx. These semicircular nerves have received the name of commissures, but a comparison with other ganglia shows that they are not the true commissures. The crura cerebri should be called the commissures. It is probable that the so-called subœsophageal commissures are nothing more than connective nerves that have united to form a semicircle about the pharynx. The following nerves arise from the supraœsophageal ganglion:—

Optic Nerves.—The small optic nerves (*o. n.*) arise the most cephalad of any of the nerves from the supraœsophageal ganglion and without branching extend to the groups of ocelli on each side of the head where they break up into small branches and supply each ocellus.

Antennal Nerves.—The antennal nerves (*at. n.*) are of about the same size as the optic nerves and arise from the ganglion caudad of and adjacent to the optic nerves, and extend cephalad and ventrad. Not far from the ganglion, they fork and form two branches, one of which innervates the area at the base of the antenna and the other the antenna itself.

Clypeo-Labral Nerves.—The pair of clypeo-labral nerves (*cl. lr. n.*) are the most caudal pair of the nerves arising from this region of the supraœsophageal ganglion. Each clypeo-labral nerve gives rise to several cephalo-mesal extending nerves and one caudo-lateral branch. The latter branch, arises from the clypeo-labral nerve in a plane slightly ventrad of the frontal ganglion and terminates in an enlarged ganglion-like structure on the labral aspect of the pharynx. This ganglion-like structure gives rise to several small nerves. The first cephalo-mesal branch from the clypeo-labral nerve is very short and arises in a plane slightly dorsad of the frontal ganglion. The succeeding or second cephalo-mesal nerve from the clypeo-labral nerve connects with the Y-shaped branch given off from the frontal

ganglion. In different specimens examined variations often occurred in respect to the exact origin of these nerves. For example, it was found that in some cases this second cephalomesal nerve arose at times ventrad of the caudo-lateral branch, while in the majority of cases it arose from the clypeo-labral nerve dorsad of the caudo-lateral branch. Further ventrad on the clypeo-labral nerves two or three other cephalomesal nerves project and innervate the cephalic area of the pharynx.

SYMPATHETIC SYSTEMS OF THE HEAD (Fig. 17 and 18).—Two sympathetic systems exist in connection with the supræoesophageal ganglion. The vagus system is an unpaired system while the sympathetic system located laterad and dorsad of the pharynx is paired.

Vagus or Unpaired Sympathetic System (Fig. 17 and 18).—The vagus system originates from the ventro-lateral part of the supræoesophageal ganglion near the clypeo-labral nerve and consists of the following parts:—

Arched Nerves.—The pair of arched nerves (*ar*) is one of the pairs of nerves which arise from the ventro-lateral area of the supræoesophageal ganglion and project ventrad on each side of the head adjacent to and somewhat cephalad of the clypeo-labral pair of nerves. They extend a short distance ventrad in a curved line then turn mesad and unite on the meson ventrad of the supræoesophageal ganglion and form a small ganglion.

Frontal Ganglion.—The enlarged, fused, mesal part of the arched nerves is the frontal ganglion (*f. g.*). It rests on the pharynx and is located caudad beneath the mouth-like opening of the aorta (Fig. 8). Nerves entrad and dorsad extending arise from this ganglion.

Frontal Nerve.—The nerve extending ventrad from the frontal ganglion is the frontal nerve (*f. n.*). It is very short and soon divides into two branches which proceed latero-ventrad for a short distance and then turn directly ventrad. At the point where they turn ventrad, the second cephalomesal branch arising from the clypeo-labral nerve fuses with them.

Recurrent Nerve.—The nerve extending dorsad on the meson from the frontal ganglion is the recurrent nerve (*r. n.*). It extends in its dorso-caudal course between the aorta and the pharynx and œsophagus (Figs. 8 and 18). As it continues its course between these organs, it follows the flexure of the pharynx so that it extends caudad as well as dorsad. In its course along

the cephalic and dorsal surface of the pharynx and œsophagus, it gives rise to paired and unpaired laterad extending branches which innervate the cephalic and dorsal parts of the pharynx and œsophagus respectively and probably also the aorta. As the recurrent nerve approaches the caudal end of the œsophagus, it divides into two branches, which pass around the side of the œsophagus.

Vagus Ganglion (Fig. 7, *v. g.*).—At the point of the forking of the recurrent nerve near the ventriculus, a minute ganglion exists, the vagus ganglion (*v. g.*).

Stomogastric Nerves (Fig. 7, *st.*).—The branches that proceed from the vagus ganglion on each side are the stomogastric nerves (*st.*). These nerves curve laterad around the œsophagus and innervate its caudal portion.

Paired Sympathetic System (Fig. 17 and 18).—On each side of the pharynx dorsad of the suprœsophageal ganglion, a sympathetic system exists, composed of two distinct nerves and two ganglia.

Lateral Nerve.—Just dorsad and slightly mesad of the large trachea that enters the suprœsophageal ganglion is the point of origin of the very small lateral nerve (*l.*). This nerve continues dorsad and slightly caudad till it ends in an enlarged, irregular, ovate-shaped ganglion on the lateral aspect of the pharynx cephalad of the subœsophageal ganglion. Running parallel with this nerve is a minute trachea which resembles a nerve very closely and is easily mistaken for one. This trachea is not indicated in Fig. 18. Often the lateral nerve, before entering the anterior, lateral ganglion, gives rise to a small branch which either connects directly with the ganglion or with the fronto-lateral nerve.

Anterior Lateral Ganglion.—The ganglion in which the lateral nerve ends, is the anterior lateral ganglion (*a. l. g.*). This ganglion gives rise on its caudal and cephalic ends to two or three nerves of various sizes which extend caudad between the muscles of the pharynx. On its dorsal margin, it gives rise to a lateral commissure (*l. c.*) which connects with the posterior lateral ganglion.

Fronto-Lateral Nerve.—The fronto-lateral nerve (*f. l.*) arises from the cephalic end of the anterior lateral ganglion adjacent to and cephalad of the point where the lateral nerve enters. The fronto-lateral nerve continues ventrad to the caudo-lateral

aspect of the supraœsophageal ganglion and connects with the ganglion by means of a short stub and then continues ventrad into the head for a considerable distance.

Lateral Commissure.—The lateral commissure (*l. c.*) is a short nerve that arises from the middle of the dorsal surface of the anterior lateral ganglion and unites with a larger ganglion dorsad and caudad of the anterior lateral ganglion. This commissure gives rise to a nerve which extends ventrad.

Posterior Lateral Ganglion.—The posterior lateral ganglion (*p. l. g.*) is larger than the anterior lateral ganglion and is located dorsad and somewhat caudad of it. It likewise gives rise to several nerves at its caudal and cephalic ends.

EXPLANATION OF PLATES.

PLATE XIX.

- Fig. 1. Lateral aspect of an entire larva of *Protoparce carolina*.
 Fig. 2. Cephalic aspect of the head.
 Fig. 3. Ventral aspect of the head.
 Fig. 4. Ventral aspect of an abdominal proleg.
 Fig. 5. Cephalic aspect of a thoracic leg.
 Fig. 6. Spiracle, enlarged.
 Fig. 7. A larva opened from the dorsal aspect showing the digestive tract. On the left the salivary glands and the tracheæ are represented which enter the canal, while on the right the malphigian tubules and silk glands are shown.
 Fig. 8. Dorsal aspect of the pharynx, enlarged.
 Fig. 9. Enlarged ventral aspect of the region of the alimentary canal, showing where the bladder of the malphigian tubule is attached.
 Fig. 10. Cells of the adipose tissue, enlarged.

PLATE XX.

- Fig. 11. A larva opened from the ventral aspect showing the respiratory system.
 Fig. 12. A larva opened from the ventral aspect showing the muscular system, circulatory system, reproductive organs, and wing buds.

PLATE XXI.

- Fig. 13. A larva opened from the dorsal aspect showing the entire nervous system.
 Fig. 14. Dorsal aspect of the seventh and eighth abdominal ganglia.
 Fig. 15. Dorsal aspect of the first abdominal ganglion.
 Fig. 16. Dorsal aspect of the metathoracic ganglion.
 Fig. 17. Dorsal aspect of the mesothoracic ganglion (*T. 2g*), prothoracic ganglion (*T. 1g*), subœsophageal ganglion (*II. 2g*), and the supraœsophageal ganglion (*II. 1g*).
 Fig. 18. Lateral aspect of the pharynx showing the nerves of the supraœsophageal and subœsophageal ganglia.

LIST OF ABBREVIATIONS.

A.	Abdomen.	md.	Mandible.
A. 1-8.	Abdominal segments one to eight.	md.-lb. n.	Mandibular-labial nerve.
a.	Anus.	md. n.	Mandibular nerve.
ad.	Adipose tissue.	m. t.	Malphigian tubule.
an.	Anal horn.	mx.	Maxilla.
a. l. g.	Anterior lateral ganglion.	mx. n.	Maxillary nerve.
ao.	Aorta.	o.	Ocelli.
ap.	Anal plate.	oe.	Esophagus.
a. pl.	Anal proleg.	o. n.	Optic nerve.
ar.	Arched nerve.	p.	Pharynx.
at.	Antenna.	pl.	Proleg.
at. n.	Antennal nerve.	p. l. g.	Posterior lateral ganglion.
b.	Bladder of malphigian tubule.	p. m.	Pharyngeal muscle.
c.	Commissure.	px.	Plexus.
c. c.	Crura cerebri.	r.	Reproductive organ.
ca.	Claw.	re.	Rectum.
ce.	Cæca.	r. n.	Recurrent nerve.
cl.	Clypeus.	r. m.	Rectal muscle.
cl. lr. n.	Clypeo-labral nerve.	s.	Spiracle.
c. n.	Connective nerve.	s. c.	Subœsophageal commissure.
co.	Coxa.	s. d.-r. m.	Small dorso-recti muscles.
d. m. t.	Dorsal malphigian tubule.	sg.	Silk gland.
d. v. m.	Dorso-ventral nerve.	s. i.	Small intestine.
e.	Epicranial suture.	sl.	Salivary gland.
f.	Front.	s. m.	Suspensory muscle.
f. b.	Mesothoracic wing bud.	s. n.	Subconnective nerve.
f. e.	Femur.	sp.	Supræesophageal ganglion.
f. g.	Frontal ganglion.	st.	Stomogastric nerve.
f. n.	Frontal nerve.	su.	Subœsophageal ganglion.
g.	Ganglion.	s. v.-r. m.	Small ventro-recti muscles.
g. d.-r. m.	Great dorso-recti muscles.	T.	Thorax.
g. v.-r. m.	Great ventro-recti muscles.	T. 1-3.	Thorax segments, prothorax, mesothorax and metathorax
H.	Head.	t.	Trachea.
h.	Heart.	ta.	Tarsus.
h. b.	Metathoracic wing bud.	ti.	Tibia.
i.	Spinneret.	t. n.	Transverse nerve.
l.	Lateral nerve.	tr.	Trochanter.
lb.	Labium.	v.	Ventral nerve.
lb. n.	Labial nerve.	ve.	Ventriculus.
l. c.	Lateral commissure.	v. g.	Vagus ganglion.
lg.	Leg.	v. m. t.	Ventral Malphigian tubule.
li.	Large intestine.	wh.	Wings of the heart.
lr.	Labrum.	x.	Unidentified muscle.
m.	Median nerve.	z.	Unidentified nerve.